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Corresponding Author: Mrs. Carolyn Jane Foley, MS

Corresponding Author's Institution: Purdue University

First Author: Carolyn Jane Foley, MS

Order of Authors: Carolyn Jane Foley, MS; Sara R Andree; Steven A Pothoven; Thomas F Nalepa; Tomas O Höök

Abstract: Invasive dreissenid mussels (*D. polymorpha* and *D. r. bugensis*) have fundamentally altered Laurentian Great Lake ecosystems, however in many areas their abundances have declined since the mid-1990s. Another invader, the benthic fish round goby (*Neogobius melanostomus*), is morphologically adapted to feed on dreissenids and likely affects dreissenid populations; however, the degree of this predatory effect is variable. In 2009 and 2010, we examined round goby abundances, size distributions, diet contents, and diet selectivity in Saginaw Bay, Lake Huron; a shallow bay that has been subjected to numerous anthropogenic stressors. We further used a consumption model to estimate dreissenid consumption by three different size classes of round goby. Round gobies were found throughout the bay and most were smaller than 80 mm total length. Round gobies of all sizes consumed dreissenids, (including fish as small as 30 mm total length), though dreissenids were rarely preferred. The relative proportion of dreissenids (by biomass) present in diets of round gobies increased with fish size, but also throughout the year for all size classes. Despite this, overall consumptive effects of round gobies on dreissenids in Saginaw Bay were low. Many dreissenids present in the bay were larger than those consumed by round gobies. Bioenergetics-based model estimates suggest that the smallest round gobies are responsible for the majority of dreissenid consumption. While our findings are limited to soft substrates and influenced by sampling restrictions, our study design allowed to put bounds on our estimates based upon these multiple sources of uncertainty.

1 Quantifying the predatory effect of round goby on Saginaw Bay dreissenids

2 Carolyn J. Foley^{a,b*}, Sara R. Andree^{a,1}, Steven A. Pothoven^c, Thomas F. Nalepa^d, Tomas O.

3 Höök^{a,b}

4 ^aPurdue University, Department of Forestry and Natural Resources, West Lafayette, IN 47906

5 ^bIllinois-Indiana Sea Grant College Program, Purdue University, West Lafayette, IN 47906

6 ^cNOAA-GLERL Lake Michigan Field Station, Muskegon, MI 49441

7 ^dWater Center, Graham Sustainability Institute, University of Michigan, Ann Arbor, Michigan

8 48104 and NOAA-GLERL, Ann Arbor, MI 48108 (emeritus)

9

10 *cfoley@purdue.edu; fax: 765-494-9461, srandree@purdue.edu, steve.pothoven@noaa.gov,

11 nalepa@umich.edu, thook@purdue.edu

12 ¹Present address: Department of Natural Resources and Environmental Sciences, University of

13 Illinois Urbana-Champaign, 1816 S. Oak St., Champaign IL, 61820.

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16 **Abstract**

17 Invasive dreissenid mussels (*D. polymorpha* and *D. r. bugensis*) have fundamentally
18 altered Laurentian Great Lake ecosystems, however in many areas their abundances have
19 declined since the mid-1990s. Another invader, the benthic fish round goby (*Neogobius*
20 *melanostomus*), is morphologically adapted to feed on dreissenids and likely affects dreissenid
21 populations; however, the degree of this predatory effect is variable. In 2009 and 2010, we
22 examined round goby abundances, size distributions, diet contents, and diet selectivity in
23 Saginaw Bay, Lake Huron; a shallow bay that has been subjected to numerous anthropogenic
24 stressors. We further used a consumption model to estimate dreissenid consumption by three
25 different size classes of round goby. Round gobies were found throughout the bay and most were
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29 throughout the year for all size classes. Despite this, overall consumptive effects of round gobies
30 on dreissenids in Saginaw Bay were low. Many dreissenids present in the bay were larger than
31 those consumed by round gobies. Bioenergetics-based model estimates suggest that the smallest
32 round gobies are responsible for the majority of dreissenid consumption. While our findings are
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34 bounds on our estimates based upon these multiple sources of uncertainty.

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37

38 **Introduction**

39 The introduction of zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena r.*
40 *bugensis*, respectively) throughout the Laurentian Great Lakes has fundamentally altered food
41 webs in many ways, notably by redirecting the flow of nutrients from pelagic to benthic
42 pathways (Hecky et al. 2004, Cha et al. 2011), and altering benthic communities in terms of
43 physical structure and composition (Bially and MacIsaac 2000, Zhu et al. 2006, Ward and
44 Ricciardi 2007). After being first reported in Lake St. Clair in 1988 (Hebert et al. 1989), zebra
45 mussels dispersed rapidly among the Great Lakes and throughout the U.S. and Canada (Benson
46 2013). However, observed peak densities have varied widely from region to region, spanning
47 several orders of magnitude (Benson 2013). This variation is likely influenced by substrate type,
48 as zebra mussels prefer hard substrates to which they can more firmly attach (Marsden and
49 Lansky 2000), and are generally less abundant on sand and silt (Wilson et al. 2006). Zebra
50 mussel expansion in North America has often been closely followed by that of the invasive
51 quagga mussel. This congeneric species has not only impacted zebra mussel populations, but
52 also come to dominate benthic communities in many habitats where zebra mussels were rarely
53 found (Nalepa et al. 2010, Benson 2013). Quagga mussels are able to colonize softer, less
54 structured substrates, and can tolerate and reproduce at lower temperatures (Diggins 2001,
55 Garton et al. 2013). Lower respiration requirements (Stoeckmann 2003) and comparatively more
56 efficient filtration capacity at low food densities (Baldwin et al. 2002, Diggins 2001) and in the
57 presence of predators (Naddafi and Rudstam 2013) have likely also facilitated quagga mussel
58 proliferation throughout the Great Lakes.

59 Though dreissenids have become dominant members of Great Lakes ecosystems, recent
60 declines in dreissenid density and condition have become apparent in lakes Michigan, Huron,

61 Erie, and Ontario (Glyshaw et al. 2015, Karatayev et al. 2014, Nalepa et al. 2010, Pennuto et al.
62 2012a). Potential explanations for these decreases include that dreissenids have reached carrying
63 capacity and are now food-limited (Bunnell et al. 2013, Hecky et al. 2004, Wilson et al. 2006);
64 have been negatively influenced by coldwater upwellings in nearshore areas (Wilson et al. 2006)
65 or, (especially for quagga mussels), are being preyed upon (Naddafi and Rudstam 2013, Naddafi
66 and Rudstam 2014a). Dreissenids serve as prey for a variety of native fish species, including lake
67 whitefish (*Coregonus clupeformis*) (Madenjian et al. 2010), yellow perch (*Perca flavescens*)
68 (Morrison et al. 1997, Roswell et al. 2013, Withers et al. 2014), freshwater drum (*Aplodinotus*
69 *grunniens*) (Morrison et al. 1997) and common carp (*Cyprinus carpio*) (French 1993), and
70 predation by fishes may be an increasingly important factor influencing dreissenid abundance.
71 Past research in the Great Lakes suggests that round gobies may be particularly effective at
72 culling dreissenid populations (Lederer et al. 2008, Naddafi and Rudstam 2014b, Wilson et al.
73 2006). The extent and impact of round goby predation upon dreissenids may vary spatially
74 throughout the Great Lakes Basin (Kipp et al. 2012), and there is an ongoing need to examine the
75 ability of round goby predation to affect dreissenid abundance across a variety of ecosystems
76 (Ruetz et al. 2012).

77 Round gobies possess a suite of life history traits (e.g., multiple annual reproductive
78 episodes) and behavioral strategies (e.g., nest-guarding and aggression) which allow them to
79 successfully reproduce and thrive in shallow, warmer regions of the Great Lakes (Vanderploeg et
80 al. 2002). Additionally, their preference for hard substrates as feeding and nesting sites (Ray and
81 Corkum 2001) and the presence of both upper and lower pharyngeal teeth (Ghedotti et al. 1995)
82 likely make them particularly adept at exploiting dreissenids as a food source. Previous studies
83 confirm that dreissenids can comprise a large proportion of round goby diets, especially for

84 larger individuals with fewer morphological limitations (French and Jude 2001, Lederer et al.
85 2008, Ray and Corkum 1997). Some research suggests that round goby predation can drastically
86 reduce dreissenid abundance; in Lake Erie, Barton et al. (2005) observed a 94% reduction of
87 dreissenid density from 2002-2004, which coincided with increasing round goby predation upon
88 dreissenids. Conversely, other studies estimate that round goby predation affects only a small
89 portion of dreissenid populations in Lakes Erie (Bunnell et al. 2005, Johnson et al. 2005b) and
90 Ontario (Pennuto et al. 2012a). Evidence also suggests that smaller round gobies tend to prefer
91 non-dreissenid prey (Barton et al. 2005, Diggins et al. 2002). An ontogenetic diet shift (occurring
92 between 60-100 mm total length) from soft-bodied macroinvertebrates to almost exclusively
93 molluscs is typical of round gobies in both their native and invasive ranges (Janssen and Jude
94 2001, Jude et al. 1995), and is likely regulated by progressive development of the pharyngeal
95 feeding apparatus (Andraso et al. 2011a).

96 Saginaw Bay, a large, shallow embayment of Lake Huron, has undergone many changes
97 due to both anthropogenic activity (Fielder et al. 2000, Johengen et al. 2000), and multiple
98 introductions of nonindigenous species (e.g., Fielder and Thomas 2006, Ivan et al. 2014).
99 Saginaw Bay remains the largest Area of Concern of the Great Lakes, being persistently
100 impacted by beneficial use impairments including eutrophication, loss of fish and wildlife
101 habitat, and population degradation of fish, wildlife and benthic invertebrates (Selzer et al.
102 2014). While various remedial activities have begun to ameliorate these conditions, the bay has
103 yet to fully recover and remains an area of unique and ongoing management interest (Selzer et al.
104 2014). One continued concern is that the bay's benthic habitat remains largely altered by the
105 presence of dreissenids (Nalepa et al. 2003). Mean density and biomass of dreissenids on hard
106 substrates in Saginaw Bay declined dramatically between the early-to-mid-1990s and 2008-2010.

107 After wide-scale, annual fluctuations in the immediate years after initial establishment, the
108 population stabilized, and in 1993-1996 mean density and shell-free, ash-free dry weight biomass
109 was 4,163/m² (SE= 747/m²) and 7.6 g/m² (SE=2.2 g/m²) (Nalepa et al 2003). However, by
110 2008-2010 mean density and biomass was only 922/m² (SE=444 g/m²) and 1.6 g/m² (SE=0.2
111 g/m²) (Nalepa et al. *In prep*).

112 As in other systems, the decrease in dreissenid populations over hard substrates in
113 Saginaw Bay was coincident with an increase in round goby size and abundance (Schaeffer et al.
114 2005). In 2009 and 2010, round gobies were the third most abundant fish caught in annual fall
115 trawling surveys (Fielder and Thomas 2014). They have become an increasingly important
116 member of the Saginaw Bay fish community, with CPE increasing up to 2-fold between 1997
117 and 2003 (Fielder and Thomas 2014, Schaeffer et al. 2005), and continuing to increase since
118 2005 even as many native prey fish species have declined (Ivan et al. 2014, Fielder and Thomas
119 2014). Whether or not round gobies have a major effect on dreissenid populations in Saginaw
120 Bay has been posited (Nalepa et al. 2003), but to date has not been evaluated. The objectives of
121 this study were to infer the predatory effect of round gobies on dreissenid populations in
122 Saginaw Bay by 1) examining round goby feeding patterns in terms of diet composition and prey
123 preference, and 2) estimating round goby consumption of dreissenids and relating this to overall
124 dreissenid population characteristics (e.g., size, abundance, production).

125

126 **Methods**

127 *Field and laboratory methodology*

128 We collected round gobies and potential prey from five sites in Saginaw Bay (Figure 1),
129 which varied in depth and sediment type (Table 1). We attempted to visit each site once per
130 month, from April through November in 2009 and 2010. We collected fish during the day with a
131 7.62 m headrope, 4-seam bottom trawl with a 3.175 mm mesh cod liner, performing 3-7 trawls
132 per site visit. We calculated the area sampled by each trawl by recording start and end
133 coordinates using a GPS unit, then estimating distance travelled using the point distance tool in
134 ArcGIS (ESRI 2011). Trawl doors do not always fully open, thus we conservatively assumed
135 that the trawl opened halfway during each tow, and multiplied the distance travelled during a
136 trawl by 3.81 m to calculate the area sampled by each trawl (m²). Immediately after collection,
137 round gobies were separated from all other fish collected, frozen in water and stored at -20°C
138 until processing. Dreissenids and other benthic macroinvertebrate taxa were collected with
139 duplicate PONAR grabs (0.052 m² opening) either directly before or after trawling. We rinsed
140 PONAR samples through a 500 µm mesh bucket in the field and preserved contents in 10%
141 formalin with rose Bengal stain. Sediment type was determined by examining the contents of the
142 PONAR. We also recorded depth of the site (m), surface temperature (°C) and day of year of
143 sampling (DOY).

144 Fish and invertebrate samples were processed in the laboratory within one year of
145 collection. All round gobies were thawed and counted, and up to 30 randomly-selected
146 individual fish per trawl tow were measured (to nearest mm) and weighed (to nearest 0.01 g).
147 From each trawl, we randomly selected round gobies for diet analysis (up to 20 round gobies per
148 site per month, spread evenly across trawls collected during a single sampling event). Since
149 round gobies have no distinct stomach, we thawed, measured and weighed each fish, then
150 removed the fish's entire digestive tract (after Barton et al. 2005, MacInnis and Corkum 2000).

151 Under a dissecting microscope, we identified (to lowest possible taxonomic level) and counted
152 all diet items with a head or complete shell, and then photographed and measured each item to
153 the nearest 0.1 mm using Image J analysis software (Schneider et al. 2012). We estimated dry
154 weight (DW) of individual diet items using published length-weight relationships or mean dry
155 weight (Roswell 2011). From these, we calculated the proportion by biomass of dreissenids
156 consumed by individual round gobies.

157 We processed benthic macroinvertebrate samples in the laboratory by rinsing with water
158 through a 500 μm mesh sieve and transferring contents to a sorting tray. We examined the tray
159 under a magnifying lamp and removed, identified and counted all whole benthic
160 macroinvertebrates, as well as those with identifiable heads. Animals were then stored in 70%
161 ethanol. We photographed and measured up to 20 randomly selected dreissenids per sample with
162 a dissecting microscope, camera, and ImageJ analysis software (Schneider et al. 2012). In some
163 samples, we observed very large numbers of 1-3 mm individuals. For these, we photographed
164 and measured 20 of these smaller individuals and up to 20 larger individuals. Dreissenids that
165 were too large to photograph were measured to the nearest mm using a ruler under a dissecting
166 microscope. To estimate biomass, we converted lengths to shell-free dry weights (mg) using
167 published length-weight regressions for quagga ($W = 0.0078L^{2.783}$; Conroy et al. 2005) and zebra
168 ($W = 0.007L^{2.982}$; Mackie 1991) mussels, determined the mean weight of each taxon, and
169 multiplied the mean weight by the mean density of animals of the taxon in that sample.

170 *Statistical and selectivity analyses*

171 To understand potential differences in round goby feeding over the year, we performed
172 an ANCOVA with mean size of dreissenid found in round goby diets as the response variable,
173 month (May, July and September only) as the explanatory variable, and total length of individual

174 fish (mm) as the covariate. We also performed ANOVAs on the mean proportion of dreissenids
175 relative to other items found in round goby diets of three distinct size classes (TL) that
176 correspond roughly to age classes (< 70 mm = Age-0, 71-88 mm = Age-1, > 88 mm = Age-2 and
177 older; e.g., MacInnis and Corkum 2000, Taraborelli et al. 2010), with year, month (May, July
178 and September) and size class as between group factors. Proportion data were $\ln+0.001$
179 transformed prior to analyses, and all analyses were performed using the ezANOVA package in
180 R (R Core Team 2013).

181 To investigate feeding preference, we evaluated selectivity of round gobies for various
182 benthic macroinvertebrate prey by calculating Chesson's α (Chesson 1983), as defined by the
183 equation

$$\alpha = \frac{r_i/p_i}{\sum_i r_i/p_i}$$

184 where r_i is the proportion (by count) of a prey type found in diets, and p_i is the proportion (by
185 density per m^2) found in the environment. Prey availability varied with site and season of
186 sampling (C. Foley, unpublished data), thus values of α were calculated for individual sites each
187 month for which data were available. Neutral selection for each site was determined as one
188 divided by the average of all α values for each site (Chesson 1983). Prey items were grouped into
189 eight categories which included all macroinvertebrates observed in both diets and the
190 environment. The category "Chironomidae" included both larvae and pupae of this taxon, and
191 the category "Dreissenidae" included both zebra and quagga mussels. The number of fish
192 included in these site-month calculations ranged from 1 to 34.

193 *Estimates of consumption*

194 Bioenergetics models have often been used to estimate predatory demand on prey taxa
195 (e.g., Johnson et al. 2005b, Stewart and Ibarra 1991). Lee and Johnson (2005) developed a
196 temperature- and weight-dependent bioenergetics model for round goby in the Great Lakes. We
197 applied this model (using Saginaw Bay-specific data) to estimate round goby consumption under
198 three scenarios (see below). Given that round gobies spawn multiple times per year, it is difficult
199 to follow growth of distinct cohorts and age classes. In addition, in North America, different age
200 classes of round goby often overlap in size (e.g., MacInnis and Corkum 2000, Taraborelli et al.
201 2010). In order to assess the potential effect of round goby predation on dreissenid populations,
202 we placed an upper bound on potential round goby consumption by assuming that round gobies
203 were feeding at their maximum daily rate (as estimated by Lee and Johnson 2005) for a given
204 weight and temperature (after Ryan et al. 2013).

205 We estimated densities of round gobies per trawl for the three different size classes
206 (previously described) as well as total round goby catch. For trawls in which more than 30 round
207 gobies were caught (i.e., not all fish were measured), we multiplied total round goby catch by the
208 proportion of fish of a given size class in the subset of fish measured. However, by collecting
209 fish via trawls and sampling some sites dominated by soft substrates, we expect that we
210 underestimated both the true abundances and size distributions of round gobies present in the bay
211 (Steingraeber et al. 1996, Wilson et al. 2006, Young et al. 2010). Round gobies may be able to
212 escape trawls as they move horizontally, or even underneath the trawl. Previous studies have
213 argued that video recordings are the most appropriate way to estimate round goby abundance
214 (Johnson et al. 2005a, Ray and Corkum 2001), though round goby densities may still be
215 underestimated by up to 60X (Ray and Corkum 2001). Round gobies have been found in lower
216 densities over sandy substrates (e.g., Johnson et al. 2005a, Pennuto et al. 2012b) and smaller

217 sizes when caught in trawls versus other types of sampling gear (e.g., Clapp et al. 2001,
218 Steingraber et al. 1996). Given this, our density estimates are likely lower than would be
219 attributed via other methods (i.e, scuba surveys or video recordings over a relatively small area).

220 We estimated potential total consumption (g) by round gobies of three different size
221 classes (< 70 mm, 71-88 mm, and > 88 mm) per m² from May 1 through November 1 of 2009
222 and 2010. To determine daily temperatures for each year, we fit a polynomial equation to
223 observed surface temperature data (Supplementary Material). Inner Saginaw Bay is generally
224 well-mixed and not thermally stratified (Nalepa et al. 2003), thus we assume that surface
225 temperatures are roughly the same as those at the bottom, where round gobies typically reside.
226 We then estimated the daily total consumption (g) of a mean-sized individual round goby for
227 each size class for each day (daily mean weight determined by linearly interpolating mean
228 weight between sampling days). This base value we call C_{Daily}. We then modified C_{Daily} for each
229 size class according to the following scenarios:

- 230 1. “Observed conditions”: C_{Daily}*Observed proportions of dreissenids in
231 diets*Observed densities of round gobies
- 232 2. “Only dreissenids consumed” (proportions of dreissenids in diets = 1):
233 C_{Daily}*1*Observed densities of round gobies
- 234 3. “Alternate round goby density”: C_{Daily}*Observed proportions of dreissenids in
235 diets*10,000*Observed densities of round gobies

236 Daily densities of each size class of round goby were determined by linearly interpolating
237 mean density between sampling days for each year. For the “Alternate round goby density”
238 scenario, we sought to modify our round goby density estimates to densities similar to those
239 observed by others in the Laurentian Great Lakes via non-trawl sampling methods (typically

240 swimming over 100-200 m transects; see Table S1 in Supplementary material). The
241 multiplication factor to achieve this was 10,000X. For the “Observed conditions” and “Alternate
242 round goby density” scenarios, we linearly interpolated the mean proportion of dreissenids
243 present in round goby diets of each size class from May through July and July through
244 September (Supplementary material). Given that we did not examine diet contents of round
245 gobies collected in October or November, we assumed that the proportion of dreissenids
246 consumed by an individual in each size class remained constant from September 1 through
247 November 1. We summed the dreissenid consumption estimates (g/m^2) for each scenario and
248 size class from May 1 to November 1 of each year, resulting in potential annual consumption
249 estimates for dreissenids in $\text{g}/\text{m}^2/\text{year}$.

250 We compared the potential annual consumption estimates to estimates of annual
251 dreissenid production in inner Saginaw Bay. Production-to-biomass (P/B) ratios are used to
252 understand how a population is replacing itself over time. To estimate mean wet biomass (g/m^2)
253 of dreissenids in Saginaw Bay, we multiplied mean wet weight plus shells of dreissenids by the
254 mean number of dreissenids per m^2 (over all sites and months sampled) for 2009 and 2010. P/B
255 values for dreissenids are scarce in general (Mackie and Schloesser 1996), but particularly so for
256 populations from the Laurentian Great Lakes. Johannsson et al. (2000) used shell-free wet
257 weight (WW) of dreissenids to calculate a P/B ratio of 5.3 for quagga mussels in Lake Erie. For
258 our production estimate, we adjusted shell-free dry weight dreissenid biomass estimates
259 previously calculated by converting dreissenid dry weight to wet weight (DW=8.2%WW for
260 quagga mussels, DW=7.1%WW for zebra mussels; from site M-25, year 2004, in Nalepa et al.
261 2010). To make results comparable to round goby consumption estimates, we added shell weight
262 to each dreissenid by multiplying shell length by 8.4 for quagga mussels and 14.2 for zebra

263 mussels (shell length: shell weight ratios taken from site M-25, year 2004, in Nalepa et al. 2010).
264 After calculating mean wet weights plus shells of dreissenids per m² for each year, we multiplied
265 by 5.3 (Johannsson et al. 2000) to determine dreissenid production in g/m²/year.

266

267 **Results**

268 Both round gobies and dreissenids were found ubiquitously throughout the bay during
269 both years (Table 2). Overall round goby densities and catch-per-unit-effort in terms of fish
270 caught per hour trawled varied from month to month and were highest at sites 2, 5 and 14 (i.e.,
271 hard-bottomed and/or primarily sandy sites), in June through September (Table 2). The round
272 gobies caught in our trawls were typically smaller than 80 mm (Figure 2) but ranged from 20 to
273 135 mm total length. Dreissenid densities were largely stable throughout each year and were also
274 highest at sites 2, 5 and 14 (with one instance of very high densities at site 10 in September;
275 Table 2). The overall makeup of all dreissenids sampled via PONARs was approximately 11%
276 zebra mussel, 89% quagga mussel (by count).

277 Round goby diet composition varied among months and size classes (Figure 3).
278 Chironomids accounted for the bulk of diet biomass estimates in most cases, occurring in diets
279 during every season and in each size class. Round gobies usually did not prefer dreissenids over
280 other available prey items (Figure 4), and only selected for dreissenids in ~15% of all instances
281 analyzed. In 2009, round gobies selected for dreissenids during June (neutral selection = 0.25,
282 $\alpha_{\text{dreissenid}} = 0.99$) and October (neutral selection = 0.33, $\alpha_{\text{dreissenid}} = 0.99$), both at site 10. In 2010,
283 round gobies selected dreissenids during May at sites 5 (neutral selection = 0.2, $\alpha_{\text{dreissenid}} = 0.83$)
284 and 20 (neutral selection = 0.25, $\alpha_{\text{dreissenid}} = 0.71$), during July at 20 ($\alpha_{\text{dreissenid}} = 1$), and during

285 September at 2 (neutral selection = 0.33, $\alpha_{\text{dreissenid}} = 0.98$). Chironomids were the most often
286 preferred prey type, being positively selected ~78% of the time (over all instances analyzed).
287 Other taxa that were preferred include amphipods (~23% of the time), gastropods, sphaeriids,
288 and other, non-chironomid insects (<1% of the time each, Figure 4).

289 Though not preferred, dreissenids were consumed by round gobies of all size classes
290 (Figure 3). Only one zebra mussel was found in all round goby diets examined, thus the vast
291 majority of dreissenids consumed were quagga mussels. The mean number of dreissenids found
292 in an individual round goby diet was 1.6 (SD=3.7) in 2009, and 2.1 (SD=5.6) in 2010. We found
293 dreissenids in 39% and 42% of round goby diets from 2009 and 2010, respectively. The mean
294 proportion of dreissenids in diets (by biomass; Table 3) was significantly different by size class
295 ($F_{2, 380}=14.8$, $p<0.001$) but not month ($F_{2, 380}=1.9$, $p=0.15$) or year ($F_{1, 380}=0.2$, $p=0.65$). The
296 largest round gobies had the highest proportion of dreissenids in diets (Figure 3, Table 3), and, in
297 general, larger round gobies also consumed larger dreissenids (Figure 5). The overall mean (and
298 range) of dreissenid shell lengths found in round goby diets was 3.4 mm (0.5-14.3 mm).
299 Including total length of round goby as a covariate, there were significant differences in mean
300 size of dreissenid consumed across months ($F_{2, 163}=3.3$, $p=0.04$) but not years ($F_{1, 163}=0.17$,
301 $p=0.68$). In both years, round gobies consumed smaller dreissenids in May than in July or
302 September. There was greater distinction between mean size of dreissenids consumed in July and
303 September in 2009 than in 2010 (Figure 5). This may be due in part to a large number of very
304 small (i.e., 2-3 mm) dreissenids observed in 2010 samples (C. Foley, unpublished data). Size
305 distributions of dreissenids found in round goby diets closely patterned those available in the
306 environment, up to about 10 mm (Figure 6).

307 The mean shell-free wet weight biomass of dreissenids for all sites and months sampled
308 was 210 g/m² in 2009 and 168 g/m² in 2010. Adding in shells resulted in a mean biomass of 339
309 g/m² in 2009 and 268 g/m² in 2010. Total annual consumption estimates for individuals from
310 each size class (Table 3) were similar to those calculated by Lee and Johnson (2005) for Lake
311 Erie (17.19 g/m² for Age-0, 49.34 g/m² for Age-1, 108.09 g/m² for Age-2). Model estimates of
312 potential total consumption of dreissenids by round gobies in inner Saginaw Bay under observed
313 conditions were several orders of magnitude lower than the estimates of annual dreissenid
314 production for both years and all size classes (Table 3). Assuming round gobies consumed
315 nothing but dreissenids led to increases in total dreissenid consumption for all size classes, but
316 estimates still fell far below production estimates (Table 3). Assuming alternate densities of
317 round gobies resulted in the greatest increase in consumption estimates (Table 3). Under this
318 scenario, estimates of total round goby consumption of dreissenids was 19% of annual dreissenid
319 production in 2009 and 27% of annual dreissenid production in 2010. For all scenarios,
320 consumption of dreissenid biomass by the smallest (and most abundant) size class of round goby
321 was higher than consumption of dreissenid biomass by either of the other two size classes (Table
322 3).

323 **Discussion**

324 Round gobies and dreissenids overlapped temporally and spatially in Saginaw Bay,
325 suggesting potential for round goby predation on dreissenid populations. However, low round
326 goby densities at particular locations and certain times of year (presumably due to offshore
327 movement overwinter, e.g., Ray and Corkum 2001) may lead to decreased predatory effect on
328 dreissenids. Similar to findings from other relatively warm and shallow areas of the Laurentian
329 Great Lakes (e.g., Barton et al. 2005, Lederer et al. 2008), dreissenids were not the primary prey

330 for round gobies collected by our study. We did observe a shift toward greater proportion of
331 dreissenids with increasing round goby total length (as in Janssen and Jude 2001, Jude et al.
332 1995), however dreissenids comprised little more than half of total diet contents for even the
333 largest round gobies collected. Chase and Bailey (1999) suggested that quagga mussels would be
334 more vulnerable to predation than zebra mussels, and our results support this. By counting whole
335 dreissenid shells only, we have likely underestimated the total biomass of dreissenids consumed
336 (Hamilton 1992). However, given that dreissenid shells break down more slowly than other
337 invertebrate prey, it is also possible that we have underestimated the importance of non-
338 dreissenid prey to round goby diets (Brush et al. 2012).

339 Dreissenids of various sizes were available in the environment, but round gobies seem to
340 focus predation on dreissenids smaller than 10 mm. We also observed no dreissenids larger than
341 14.3 mm in any round goby diets. Together, these findings complement previous suggestions that
342 predators of dreissenids select individuals from a relatively narrow size range (8-11 mm; e.g.
343 Andraso et al. 2011b, Ray and Corkum 1997). Naddafi and Rudstam (2014b) found that, while
344 larger round gobies were capable of consuming dreissenids up to 20 mm, they preferred
345 dreissenids between 4-8 mm; furthermore, other predators including pumpkinseed sunfish
346 (*Lepomis gibbosus*) and rusty crayfish (*Oronectes rusticus*) were only able to consume
347 dreissenids that were smaller than 8 mm. Morrison et al. (1997) observed a similar preference for
348 dreissenids of only 2-6 mm, even by large yellow perch and freshwater drum. In Saginaw Bay,
349 round gobies may be gape-limited predators of dreissenids, given that size distributions of
350 dreissenids up to 10 mm are fairly similar between the environment and those found in round
351 goby diets (i.e., round gobies do not appear to prefer particular sizes, but rather consume what is
352 available). As a result, it seems that many dreissenids in Saginaw Bay have grown to sizes

353 essentially invulnerable to most round goby predation. Given that dreissenids invest similarly in
354 reproduction throughout their adult lifespans (Stoeckmann 2003) and are considered sexually
355 mature at approximately 8-9 mm in length (Benson et al. 2016), the selective cropping of smaller
356 individuals by round gobies may not have a pronounced impact on overall dreissenid population
357 reproductive ability; especially as thinning of small dreissenids may allow release from density-
358 dependent control and allow for faster growth.

359 While round gobies often selected for other prey items, they did at times select for
360 dreissenids. These instances did not share common sites or dates, nor did they always coincide
361 with sampling events where we collected greater numbers of large round gobies (which would be
362 expected to prey most heavily on dreissenids). In 2010, round gobies seemed to select more
363 strongly for dreissenids when observed dreissenid abundance was relatively low. It is possible
364 that lower abundances, and thus smaller aggregations, of dreissenids allowed round gobies to
365 more easily harvest individuals that may otherwise have been covered or wedged between larger
366 dreissenids (Andraso et al. 2011b, Ghedotti et al. 1995). However, it also seems plausible that the
367 perceived preference is simply an artifact of the selectivity calculation itself, i.e., similar
368 numbers of dreissenids were consumed by round gobies in these areas as in other areas where the
369 number of available dreissenids was greater.

370 Even though small round gobies consume fewer dreissenids on an individual basis, our
371 model estimates suggest that their high abundances may ultimately lead to much greater overall
372 consumption of dreissenid biomass than their larger counterparts. One caveat is that our annual
373 consumption estimate excludes the months of November through April. While numbers of round
374 gobies captured did decline during cooler months, presumably due to offshore movement (e.g.,
375 Ray and Corkum 2001), and consumption estimates would likely decrease in cooler temperatures

376 (Lee and Johnson 2005), individual round gobies may continue to prey on dreissenids during this
377 time period. Another previously mentioned caveat is that we have sampled softer substrates with
378 gear that is not ideal for assessing round goby densities. Our calculations of fishing effort in
379 terms of number of round gobies caught per trawl hour are similar to those found by others
380 sampling the Great Lakes (e.g., Clapp et al. 2001, Steingraeber et al. 1996), and the relative
381 frequencies of round gobies of particular sizes reflected in our study are comparable to those
382 presented by Schaeffer et al. (2005), Fielder and Thomas (2006), and Cooper et al. (2009) for
383 Saginaw Bay. Schaeffer et al. (2005) and Fielder and Thomas (2006) presented data from the late
384 1990s to mid-2000s, while Cooper et al. (2009) presented data from 2006. Two of these studies
385 also present trawl data, and thus may have the same biases toward smaller-bodied round gobies
386 as previously noted; however, Cooper et al. (2009) sampled using overnight fyke nets which
387 would presumably be less biased. While multiple studies have described a size structure of round
388 gobies similar to that found in our study, specifically targeting larger round gobies in order to
389 assess both their abundances and dreissenid consumption patterns would be necessary before
390 fully assessing predatory effects of round gobies.

391 Examining multiple scenarios with bioenergetics modeling allowed us to assess how
392 uncertainty regarding round goby densities and prey consumption might influence their potential
393 predatory impact. In Saginaw Bay, the most sensitive variable by far was round goby density,
394 while uncertainty in consumption rate or diet composition were less influential. The vulnerability
395 (or lack thereof) of round gobies to certain sampling methods makes it difficult for researchers to
396 assess the role of this relatively new invader in Great Lakes food webs. We therefore emphasize
397 the need for improved, less biased collection methods for round gobies. Another source of
398 uncertainty in our study is the P/B ratio of the dreissenid population. The P/B ratio calculated by

399 Johannsson et al. (2000) for Western Lake Erie was likely calculated during the exponential
400 growth phase of that dreissenid population. P/B ratios for some zebra mussel populations in
401 Europe are much lower than this (reviewed in Chase and Bailey 1999, Mackie and Schloesser
402 1996). Chase and Bailey (1999) also found variable P/B ratios in Lake Erie, with a mean P/B
403 ratio for Lake Erie of 0.85. If we were to assume a P/B ratio of 1, the dreissenid consumption
404 estimates under the Alternate Round Goby Density scenario in each year would just exceed
405 dreissenid production as estimated over the relatively soft substrates sampled in our study.
406 However, we are likely also underestimating the total biomass of dreissenids present, given that
407 densities over hard substrates are much higher than those observed in our study (Nalepa et al.
408 2003, Nalepa et al. *In prep.*).

409 Given that many of the dreissenids sampled in our study appear to be too large to be
410 preyed upon, it seems unlikely that round goby predation has historically strongly affected
411 dreissenid populations in Saginaw Bay. At the same time, quagga mussels are becoming the
412 dominant dreissenid present in the Great Lakes and are possibly more vulnerable to predation
413 than zebra mussels (e.g., Chase and Bailey 1999, current study). We demonstrated that all sizes
414 of round goby prey on dreissenids, that round gobies consume smaller dreissenids in early parts
415 of the year (potentially exploiting the first reproductive cohort of a given year), and that round
416 gobies would likely have the greatest impact on dreissenids that are less than one year old (< 8-9
417 mm total length; Benson et al. 2016). As such, we suggest it possible that round gobies will help
418 suppress Saginaw Bay dreissenid populations in years to come. Several other fish species have
419 been known to prey on dreissenids with some regularity (e.g., Madenjian et al. 2010), and yellow
420 perch are a documented predator of dreissenids and dreissenid veligers in Saginaw Bay (Roswell
421 et al. 2013). While not assessed in the current study, it is possible that predation by other fishes

422 could act in concert with predation by round gobies, ultimately contributing to overall decline in
423 dreissenid populations.

424

425

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435

436 **References**

437 Andraso, G.M., Cowles, J., Colt, R., Patel, J., Campbell, M., 2011a. Ontogenetic changes in

438 pharyngeal morphology correlate with a diet shift from arthropods to dreissenid mussels

439 in round gobies (*Neogobius melanostomus*). *J. Great Lakes Res.* 37, 738-743.

440 Andraso, G.M., Ganger, M.T., Adamczyk, J., 2011b. Size-selective predation by round gobies

441 (*Neogobius melanostomus*) on dreissenid mussels in the field. *J. Great Lakes Res.* 37,

442 298-304.

443 Baldwin, B.S., Mayer, M.S., Dayton, J., Pau, N., Mendilla, J., Sullivan, M., Moore, A., Ma, M.,
444 Mills, E.L., 2002. Comparative growth and feeding in zebra and quagga mussels
445 (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes.
446 Can. J. Fish. Aquat. Sci. 59, 680-694.

447 Barton, D.R., Johnson, R.A., Campbell, L., Petruniak, J., Patterson, M. 2005. Effects of round
448 gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in
449 eastern Lake Erie, 2002–2004. J. Great Lakes Res. 31, S2. 252-261.

450 Benson, A.J., 2013. Chronological history of zebra and quagga mussels (Dreissenidae) in North
451 America, 1988-2010, in: Nalepa, T.F., Schloesser, D.W. (Eds.), Quagga and zebra
452 mussels: biology, impacts and control. CRC Press, Boca Raton, pp. 9-32.

453 Benson, A.J., Raikow, D., Larson, J., Fusaro, A., Bogdanoff, A.K. 2016. *Dreissena polymorpha*.
454 USGS Nonindigenous Aquatic Species Database, Gainesville, FL.
455 <http://nas.er.usgs.gov/queries/factsheet.aspx?speciesid=5> Revision Date: 6/26/2014

456 Bially, A., MacIsaac, H.J., 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in
457 Lake Erie and facilitate benthic invertebrates. Freshwater Biology. 43, 85–97.

458 Brush, J.M., Fish, A.T., Hussey, N.E., Johnson, T.B. 2012. Spatial and seasonal variability in the
459 diet of round goby (*Neogobius melanostomus*): stable isotopes indicate that stomach
460 contents overestimate the importance of dreissenids. Can. J. Fish. Aquat. Sci. 69, 573-
461 586.

462 Bunnell, D.B., Johnson, T.B., Knight, C.T., 2005. The impact of introduced round gobies
463 (*Neogobius melanostomus*) on phosphorous cycling in central Lake Erie. Can. J. Fish.
464 Aquat. Sci. 62, 15-29.

465 Bunnell, D.B., Madenjian, C.P., Desorcie, T.J., Kostich, M.J., Smith, K.R., Adams, J.V., 2013.
466 Status and trends of prey fish populations of Lake Michigan, 2012. Great Lakes Fishery
467 Commission, Duluth, MN.

468 Cha, Y., Stow, C.A., Nalepa, T.F., Reckhow, K.H., 2011. Do invasive mussels restrict offshore
469 phosphorus transport in Lake Huron? Environ. Sci. Technol. 45, 7226–7231.

470 Chase, M.E., Bailey, R.C. 1999. The ecology of the zebra mussel (*Dreissena polymorpha*) in the
471 lower Great Lakes of North America: II. Total production, energy allocation, and
472 reproductive effort. J. Great Lakes Res. 25, 122-134.

473 Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging
474 models. Ecology. 64, 1297-1304.

475 Clapp, D.F., Schneeberger, P.J., Jude, D.J., Madison, G., Pistis, C., 2001. Monitoring round goby
476 (*Neogobius melanaostomus*) population expansion in eastern and northern Lake
477 Michigan. J. Great Lakes Res. 27, 335-341.

478 Conroy, J.D., Edwards, W.J., Pontius, R.A., Kane, D.D., Zhang, H., Shea, J.F., Richey, J.N.,
479 Culver, D.A., 2005. Soluble nitrogen and phosphorus excretion of exotic freshwater
480 mussels (*Dreissena* spp.): potential impacts for nutrient remineralization in western Lake
481 Erie. Freshwater Biol. 50, 114-1162.

482 Cooper, M.J., Ruetz III, C.R., Uzarski, D.G., Shafer, B.M. 2009. Habitat use and diet of the
483 round goby (*Neogobius melanostomus*) in coastal areas of Lake Michigan and Lake
484 Huron. J. Fresh. Ecol. 24(3), 477-488.

485 Diggins, T.P., 2001. A seasonal comparison of suspended sediment filtration by quagga (*D.*
486 *polymorpha*) mussels. J. Great Lakes Res. 27, 457-466.

487 Diggins, T.P., Kaur, J., Chakraborti, R.K., DePinto, J.V., 2002. Diet choice by the exotic round
488 goby (*Neogobius melanostomus*) as influenced by prey motility and environmental
489 complexity. J. Great Lakes Res. 28 (3), 411-420.

490 ESRI, 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research
491 Institute.

492 Fielder, D.G., Johnson, J.E., Weber, J.R., Thomas, M.V., Haas, R.C., 2000. Fish population
493 survey of Saginaw Bay, Lake Huron, 1989-97. Michigan Department of Natural
494 Resources, Fisheries Report 2083, Ann Arbor.

495 Fielder, D.G., Thomas, M.V., 2006. Fish population dynamics of Saginaw Bay, Lake Huron,
496 1998-2004. Michigan Department of Natural Resources, Fisheries Research Report 2083,
497 Ann Arbor.

498 Fielder, D.G., Thomas, M.V., 2014. Status and trends of the fish community of Saginaw Bay,
499 Lake Huron 2005-2011. Michigan Department of Natural Resources, Fisheries Report
500 No. 03.

501 French, J.R.P., III., 1993. How well can fishes prey on zebra mussels in eastern North America?
502 Fisheries (Bethesda). 18, 13-19.

503 French, J.R.P., III, Jude, D.J., 2001. Diets and diet overlap of nonindigenous gobies and small
504 benthic native fishes co-inhabiting the St. Clair River, Michigan. *J. Great Lakes Res.* 27,
505 300–311.

506 Ghedotti, M.J., Smihula, J.C., Smith, G.R., 1995. Zebra mussel predation by round gobies in the
507 laboratory. *J. Great Lakes Res.* 21, 665-669.

508 Garton, D. WA. McMahon, R., Stoeckmann, A. M. 2013. Limiting environmental factors and
509 competitive interactions between zebra and quagga mussels in North America. In:
510 Nalepa, T. F. Schloesser, D. W. (Eds.) *Quagga and Zebra Mussels: Biology, Impacts, and*
511 *Control*. Second Edition. CRC Press, Boca Raton, FL, pp. 383-402.

512 Glyshaw, P. W., Riseng, C. M., Nalepa, T. F., Pothoven, S. A. 2015. Temporal trends in
513 condition and reproduction of quagga mussels (*Dreissena rostriformis bugensis*) in
514 southern Lake Michigan. *J. Great Lakes Res.* 41 (Suppl. 3): 16-26.

515 Hamilton D.J. 1992. A method for reconstruction of zebra mussel (*Dreissena polymorpha*)
516 length from shell fragments. *Can. J. Zool.* 70(12):2486-90.

517 Hebert, P.D.N., Muncaster, B.W., Mackie, G.L., 1989. Ecological and genetic studies on
518 *Dreissena polymorpha* (Pallas): a new mollusk in the Great Lakes. *Can. J. Fish. Aquat.*
519 *Sci.* 46, 1587-1591.

520 Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N.,
521 Howell, T., 2004. The nearshore phosphorous shunt: a consequence of ecosystem
522 engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61,
523 1285-1293.

524 Ivan, L. N., Fielder, D.G., Thomas, M. V., Höök, T.O., 2014. Changes in the Saginaw Bay, Lake
525 Huron, fish community from 1970-2011. *J. Great Lakes Res.* 40, 922-933.

526 Janssen, J., Jude, D.J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in
527 Calumet Harbor, southern Lake Michigan, induced by the newly introduced round
528 goby *Neogobius melanostomus*. *J. Great Lakes Res.* 27, 319–328.

529 Johannsson, O.E., Dermott, R., Graham, D.M., Dahl, J.A., Millard, E.S., Myles, D.D., LeBlanc,
530 J., 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of
531 *Dreissena* spp. with implications for fish production. *J. Great Lakes Res.* 26, 31-54.

532 Johengen, T.H., Nalepa, T.F., Lang, G.A., Fanslow, D.L., Vanderploeg, H.A., Agy, M.A., 2000.
533 Physical and chemical variables of Saginaw Bay, Lake Huron in 1994-1996. NOAA
534 Technical Memorandum no. 115, 1-5.

535 Johnson, T.B., Allen, M., Corkum, L.D., Lee, V.A., 2005a. Comparison of methods needed to
536 estimate population size of round goby (*Neogobius melanostomus*) in western Lake Erie.
537 *J. Great Lakes Res.* 31, 78-86.

538 Johnson, T.B., Bunnell, D.B., Knight, C.T., 2005b. A potential new energy pathway in central
539 Lake Erie: the round goby connection. *J. Great Lakes Res.* 31, 238-251.

540 Jude, D.J., Janssen, J., Crawford, G., 1995. Ecology, distribution, and impact of the newly
541 introduced round and tubenose gobies on the biota of the St. Clair and Detroit
542 Rivers. In: Munawar, M., Edsall, T., Leach, J. (Eds.), *The Lake Huron Ecosystem:
543 Ecology, Fisheries and Management.* : Ecovision World Monograph Series. SPB
544 Academic Publishing, Amsterdam, The Netherlands, pp. 447–460.

545 Karatayev, A.Y., Burlakova, L.E., Pennuto, C., Ciborowski, J., Karatayev, V.A., Juetten, P.,
546 Clapsadl, M. 2014. Twenty five years of changes in *Dreissena* spp. populations in Lake
547 Erie. J. Great Lakes Res. 40, 550-559.

548 Kipp, R., Hébert, I., Lacharité, M., Ricciardi, A., 2012. Impacts of predation by the Eurasian
549 round goby (*Neogobius melanostomus*) on molluscs in the upper St. Lawrence River. J.
550 Great Lakes Res. 38, 78-89.

551 Lederer, A.M., Janssen, J., Reed, T., Wolf, A., 2008. Impacts of the introduced round goby
552 (*Apollonia melanostoma*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*)
553 and on macroinvertebrate community between 2003 and 2006 in the littoral zone of
554 Green Bay, Lake Michigan. J. Great Lakes Res. 34, 690–697.

555 Lee, V.A., Johnson, T.B., 2005. Development of a bioenergetics model for the round goby
556 (*Neogobius melanostomus*). J. Great Lakes Res. 31, 125-134.

557 MacInnis, A.J., Corkum, L.D., 2000. Age and growth of round goby (*Neogobius melanostomus*)
558 in the upper Detroit River. Trans. Am. Fish. Soc. 129, 852-858.

559 Mackie, G.L., 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to
560 native bivalves and its potential impact in Lake St. Clair. Hydrobiologia. 219, 251-268.

561 Mackie, G.L., Schloesser, D.W., 1996. Comparative biology of zebra mussels in Europe and
562 North America: an overview. American Zoologist, 36, 244-258.

563 Madenjian, C.P., Pothoven, S.A., Schneeberger, P.J., Ebener, M.P., Mohr, L.C., Nalepa, T.F.,
564 Bence, J.R., 2010. Dreissenid mussels are not a “dead end” in Great Lakes food webs. J.
565 Great Lakes Res. 36, 73-77.

566 Marsden, J.E., Lansky, D.M., 2000. Substrate selection by settling zebra mussels, *Dreissena*
567 *polymorpha*, relative to material, texture, orientation and sunlight. *Can. J. Zool.* 78, 787-
568 793.

569 Morrison, T.W., Lynch, W.E. Jr., Dabrowski, K., 1997. Predation on zebra mussels by
570 freshwater drum and yellow perch in western Lake Erie. *J. Great Lakes Res.* 23, 177-189.

571 Naddafi, R., Rudstam, L.G., 2013. Predator-induced behavioural defences in two competitive
572 invasive species: the zebra mussel and the quagga mussel. *Anim. Behav.* 86, 1275-1284.

573 Naddafi, R., Rudstam, L.G., 2014a. Does differential predation explain the replacement of zebra
574 by quagga mussels? *Freshwater Sci.* 33, 895-903.

575 Naddafi, R., Rudstam, L.G., 2014b. Predator-induced morphological defences in two invasive
576 dreissenid mussels: implications for species replacement. *Freshwater Bio.* 59, 703-713.

577 Nalepa, T.F., Fanslow, D.L., Lansing, M.B., Lang, G.A., 2003. Trends in the benthic
578 macroinvertebrate community of Saginaw Bay, Lake Huron, 1987 to 1996: responses to
579 phosphorous abatement and the zebra mussel *Dreissena polymorpha*. *J. Great Lakes Res.*
580 29(1), 14–33.

581 Nalepa, T.F., Fanslow, D.L., Pothoven, S. A., 2010. Recent changes in density, biomass,
582 recruitment, size structure, and nutritional state of *Dreissena* populations in southern
583 Lake Michigan. *J. Great Lakes Res.* 36, 5-19.

584 Nalepa, T.F., Schloesser, D.W., Riseng, C.M., Baldrige Elgin, A. *In prep.* Continued changes in
585 macroinvertebrate populations within the Lake Huron system.

586 Pennuto, C.M., Howell, E.T., Lewis, T.W., Makarewicz, J.C., 2012a. *Dreissena* population
587 status in nearshore Lake Ontario. J. Great Lakes Res. 38, 161-170.

588 Pennuto, C.M., Howell, E.T., Makarewicz, J.C., 2012b. Relationships among round gobies,
589 *Dreissena* mussels, and benthic algae in the south nearshore of Lake Ontario. J. Great
590 Lakes Res. 38, 154-160.

591 R Core Team (2013). R: A language and environment for statistical computing. R Foundation for
592 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

593 Ray, W.J., Corkum, L.D., 1997. Predation of zebra mussels by round gobies, *Neogobius*
594 *melanostomus*. Environ. Biol. Fishes. 50, 267–273.

595 Ray, W.J., Corkum, L.D., 2001. Habitat and site affinity of the round goby. J. Great Lakes Res.
596 27, 329-334.

597 Roswell, C. R., 2011. Growth, condition, and diets of age-0 Saginaw Bay yellow perch,
598 implications for recruitment. MS thesis, Purdue University, West Lafayette, IN.

599 Roswell, C.R., Pothoven, S.A., Höök, T.O. 2013. Spatio-temporal, ontogenetic, and inter-
600 individual variation of age-0 diets in a population of yellow perch. Ecology of Freshwater
601 Fish. 22: 479-493.

602 Ruetz III, C.R., Reneski, M.R., Uzarski D.G. 2012. Round goby predation on *Dreissena* in
603 coastal areas of eastern Lake Michigan. J. Fresh. Ecol. 27(2), 171-84.

604 Ryan, D., Sepulveda, M.S., Nalepa, T., Ivan, L.N., Höök. 2013. A comparison of consumptive
605 demand of *Diporeia* and dreissenids in Lake Michigan based on bioenergetics models. in:
606 Nalepa, T.F., Schloesser, D.W. (Eds.), Quagga and zebra mussels: biology, impacts and
607 control. CRC Press, Boca Raton, pp. 713-724.

608 Schaeffer, J.S., Bowen, A., Thomas, M., French, J.R.P. III, Curtis, G.L., 2005. Invasion history,
609 proliferation, and offshore diet of the round goby (*Neogobius melanostomus*) in western
610 Lake Huron, USA. J. Great Lakes Res. 31, 414-425.

611 Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image
612 447 analysis. Nat. Meth. 9, 671-675.

613 Selzer, M.D., Joldersma, B., Beard, J., 2014. A reflection on restoration progress in the Saginaw
614 Bay watershed. J. Great Lakes Res. 40, S1, 192-200.

615 Steingraeber, M., Runstrom, A., Thiel, P., 1996. Round goby (*Neogobius melanastomus*)
616 distribution in the Illinois Waterway system of metropolitan Chicago. U.S. Fish and
617 Wildlife Service, Onalaska, WI.

618 Stewart, D.J., Ibarra, M., 1991. Predation and production by salmonine fishes in Lake Michigan,
619 1978-88. Can. J. Fish. Aquat. Sci. 48, 909-922.

620 Stoeckmann, A., 2003. Physiological energetic of Lake Erie dreissenid mussels: a basis for the
621 replacement of *Dreissena polymorpha* by *Dreissena bugensis*. Can. J. Fish. Aquat. Sci.
622 60, 126-134.

623 Taraborelli, A.C., Fox, M.G., Johnson, T.B., Schaner, T. Round goby (*Neogobius melanostomus*)
624 population structure, biomass, prey consumption and mortality from predation in the Bay
625 of Quinte, Lake Ontario. J. Great Lakes Res. 36, 625-632.

626 Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich,
627 I.A., Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian
628 species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59, 1209–1228.

- 629 Ward, J. M., Ricciardi, A. 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate
630 communities: a meta-analysis. *Divers. Distrib.* 13:155-165.
- 631 Wilson, K.A., Howell, E.T., Jackson, D.A., 2006. Replacement of zebra mussels by quagga
632 mussels in the Canadian nearshore of Lake Ontario: importance of substrate, round goby
633 abundance and upwelling frequency. *J. Great Lakes Res.* 32, 11-28.
- 634 Withers, J.L., T.M. Sesterhenn, C.J. Foley, C.D. Troy, Höök, T.O. 2015. Diets and growth
635 potential of early stage larval yellow perch and alewife in a nearshore region of
636 southeastern Lake Michigan. *J. Great Lakes. Res.* 41, Suppl. 3 197-209.
- 637 Young, J.A.M., Marentette, J.R., Gross, C., McDonald, J.I., Verma, A., Marsh-Rollo, S.E., Earn,
638 D.J.D., Balshine, S., 2010. Demography and substrate affinity of the round goby
639 (*Neogobius melanostomus*) in Hamilton Harbour. *J. Great Lakes. Res.* 36, 115-122.
- 640 Zhu B., Fitzgerald D.G., Mayer C.M., Rudstam L.G., Mills E.L. 2006. Alteration of ecosystem
641 function by zebra mussels in Oneida Lake: impacts on submerged macrophytes.
642 *Ecosystems.* 9(6):1017-28.

643 Table 1. Description of sample sites. Mean depth is calculated over all sampling events.
644 Temperatures are noted as mean (minimum-maximum) experienced over the sampling time
645 frame.

Site Name	Mean Depth (m)	Surface Temp. (°C)	Substrate Type
2	3.9	17.4 (5.6-26)	Rock, cobble
5	3.6	18.3 (11.7-25.9)	Cobble, gravel, sand
10	12.4	16.2 (5.6-26.9)	Silt, muck
14	3.8	18.9 (12-27.1)	Sand
20	17.7	15.2 (5.6-23.7)	Sandy silt

646

647

648 Table 2. Mean round goby (all size classes combined) and dreissenid abundances for Saginaw
 649 Bay at each site and date sampled. "--" indicates that no sampling occurred. Weather conditions
 650 completely prevented sampling during April 2009 and October 2010.

Taxon/Units	Month	Site 2		Site 5		Site 10		Site 14		Site 20	
		2009	2010	2009	2010	2009	2010	2009	2010	2009	2010
Round goby No./ha	Apr	--	2.1	--	--	--	0	--	--	--	--
	May	19.5	5.7	22.0	2.6	6.3	2.1	8.3	2.2	2.6	2.1
	Jun	93.5	--	31.8	52.6	19.8	0	76.3	--	0	--
	Jul	129	31.8	478	182	16.1	34.6	153	38.8	0	8.4
	Aug	43.2	101	21.7	897	78	58.4	177	58.2	0	99.7
	Sep	76.9	36.1	177	95.3	27.3	253	112	46.1	482	307
	Oct	16.3	--	13.0	--	241	--	70.3	--	--	--
	Nov	--	0	0	0	62.9	6.82	--	--	--	0
Round goby No./Trawl h	Apr	--	6	--	--	--	0	--	--	--	--
	May	24	18	51	6	6	6	18	6	6	6
	Jun	162	--	66	126	41	0	147	--	0	--
	Jul	299	93	698	576	32	106	345	123	0	30
	Aug	91	138	45	1857	134	141	384	156	0	290
	Sep	173	81	365	198	63	624	294	105	1,008	690
	Oct	33	--	27	--	414	--	156	--	--	--
	Nov	--	0	0	0	108	18	--	--	--	0
Dreissenids No./m ²	Apr	--	1,259	--	--	--	9.5	--	--	--	--
	May	1,735	1,821	3,185	1,316	296	0	0	114	0	114
	Jun	1,297	--	887	1,287	9.5	0	3,394	--	105	--
	Jul	1,726	1,001	591	3,194	162	0	610	467	181	76
	Aug	2,326	3,289	1,411	1,163	0	0	849	1,220	172	86
	Sep	2,220	267	2,145	6,503	1,850	0	0	601	67	0
	Oct	1,535	--	353	--	9.5	--	829	--	--	--
Nov	--	1,545	0	0	0	0	--	--	--	19	

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652

653 Table 3. Annual consumption and production estimates for Saginaw Bay, Lake Huron.
 654 Consumption estimates assume prey are shelled, wet-weight dreissenids. Production estimates
 655 are based on shell-free, wet-weight dreissenid biomass. Densities are based on distance travelled
 656 and assume the trawl opened halfway.

657

Year	Size Class	Individual Estimates			Mean No. of Round Gobies/m ²	Modeled Total Round Goby Consumption of Dreissenids (g/m ² /year)			Dreissenid Production (g/m ² /year)
		Total Consumption (g/year)	Mean Prop. Dreissenid in Diet by Biomass (by Count)	Mean Total Dreissenid Consumed (g/year)		Observed Conditions	Assume Only Dreissenids Consumed	Assume Alt. Round Goby Density	
2009	< 70 mm	17.3	0.16 (0.12)	2.8	0.008	0.023	0.16	268	1,797
	71-88 mm	42.5	0.26 (0.2)	11.1	0.00037	0.0019	0.018	46.9	
	> 88 mm	84.5	0.52 (0.39)	43.9	0.00006	0.0016	0.0049	26.1	
2010	< 70 mm	19.4	0.18 (0.18)	3.5	0.0076	0.029	0.13	289	1,416
	71-88 mm	42.2	0.24 (0.22)	10.1	0.00043	0.0042	0.016	42.2	
	> 88 mm	76.2	0.55 (0.53)	41.9	0.00011	0.0048	0.0079	47.9	

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661 Figure Captions

662

663 Figure 1. Sites in Saginaw Bay, Lake Huron from which round gobies and benthic
664 macroinvertebrates were collected in 2009 and 2010.

665 Figure 2. Length distributions of round gobies collected from Saginaw Bay, Lake Huron, by
666 month and year. A maximum of 30 fish per trawl were measured (see Methods for details).
667 Weather conditions prevented sampling in April 2009 and October 2010.

668 Figure 3. Mean proportions by biomass of diet items in three size classes of round gobies
669 collected during May, July, and September of 2009 (left) and 2010 (right) in Saginaw Bay, Lake
670 Huron. Sample sizes noted in top right corner of each plot. Prey categories are the same as those
671 included in selectivity analyses. Dreissenids are highlighted in grey.

672 Figure 4. Prey selectivity (presented as Chesson's α) of round gobies at each sampling site and
673 date for which diet information was available. Dashes indicate neutral selectivity for a given prey
674 item. Prey items that were consumed but not adequately sampled in the environment are omitted
675 from this figure, as were prey that were sampled in the environment but not observed in round
676 goby diets.

677 Figure 5. Individual round goby total length versus mean shell length of dreissenids in diets (for
678 those fish that had dreissenids in diets). Linear regressions are presented for May (solid line,
679 $n_{2009} = 12$, $n_{2010} = 4$), July (dashed line, $n_{2009} = 29$, $n_{2010} = 33$) and September (dotted line, $n_{2009} =$
680 53 , $n_{2010} = 48$).

681 Figure 6. Length distributions of dreissenids collected from the environment (via PONAR) and
682 observed in round goby diets.

Figure 1
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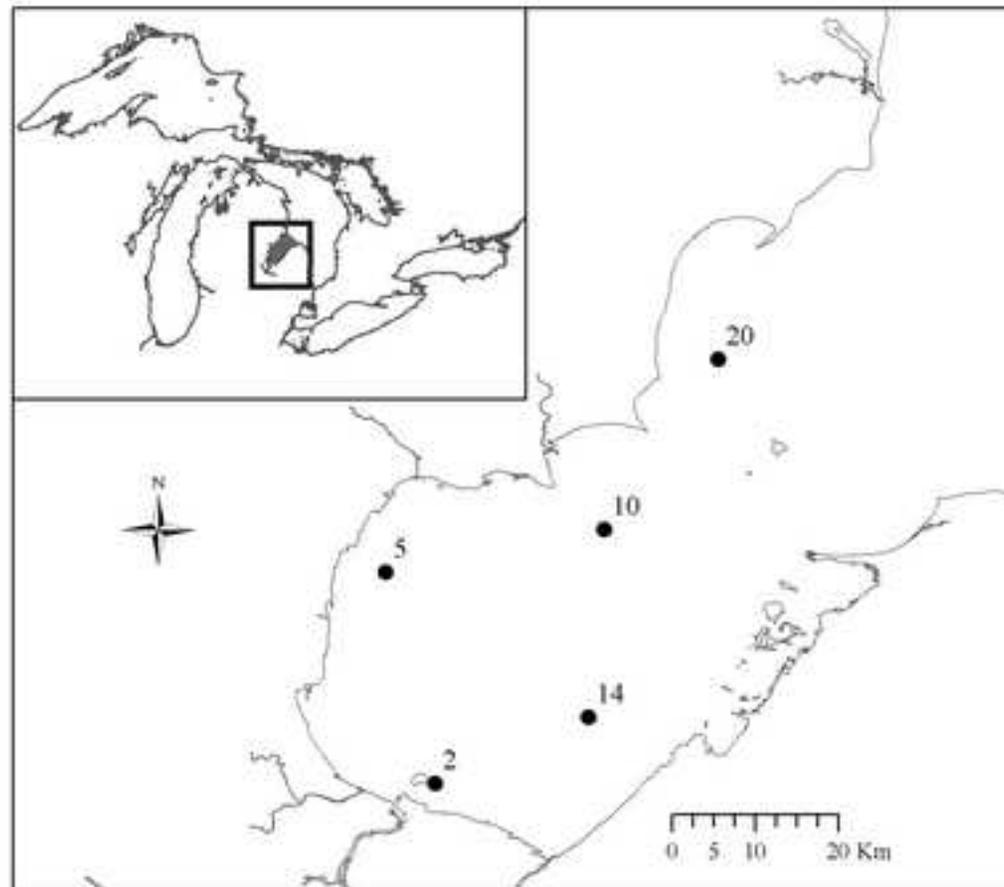


Figure 2

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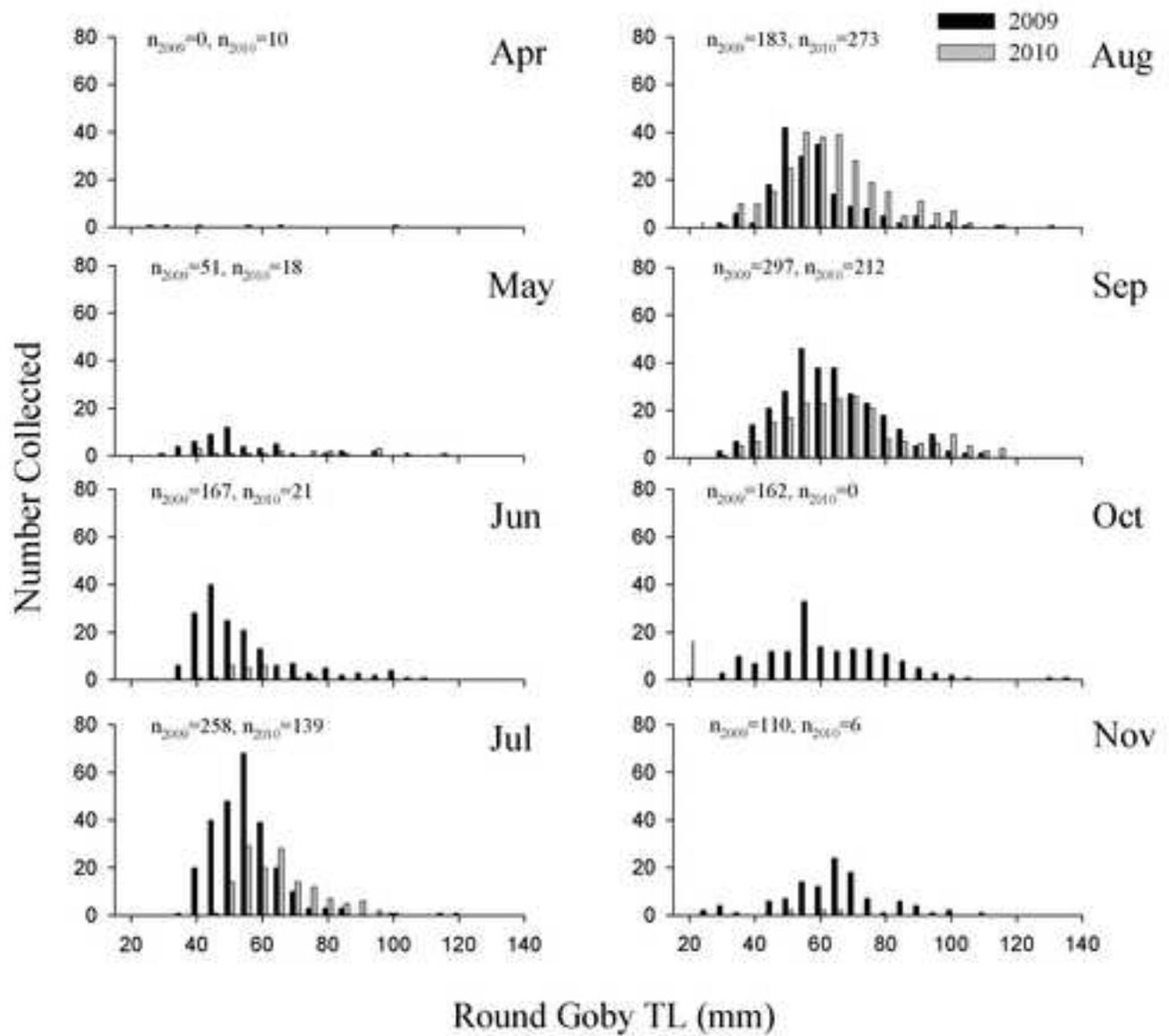


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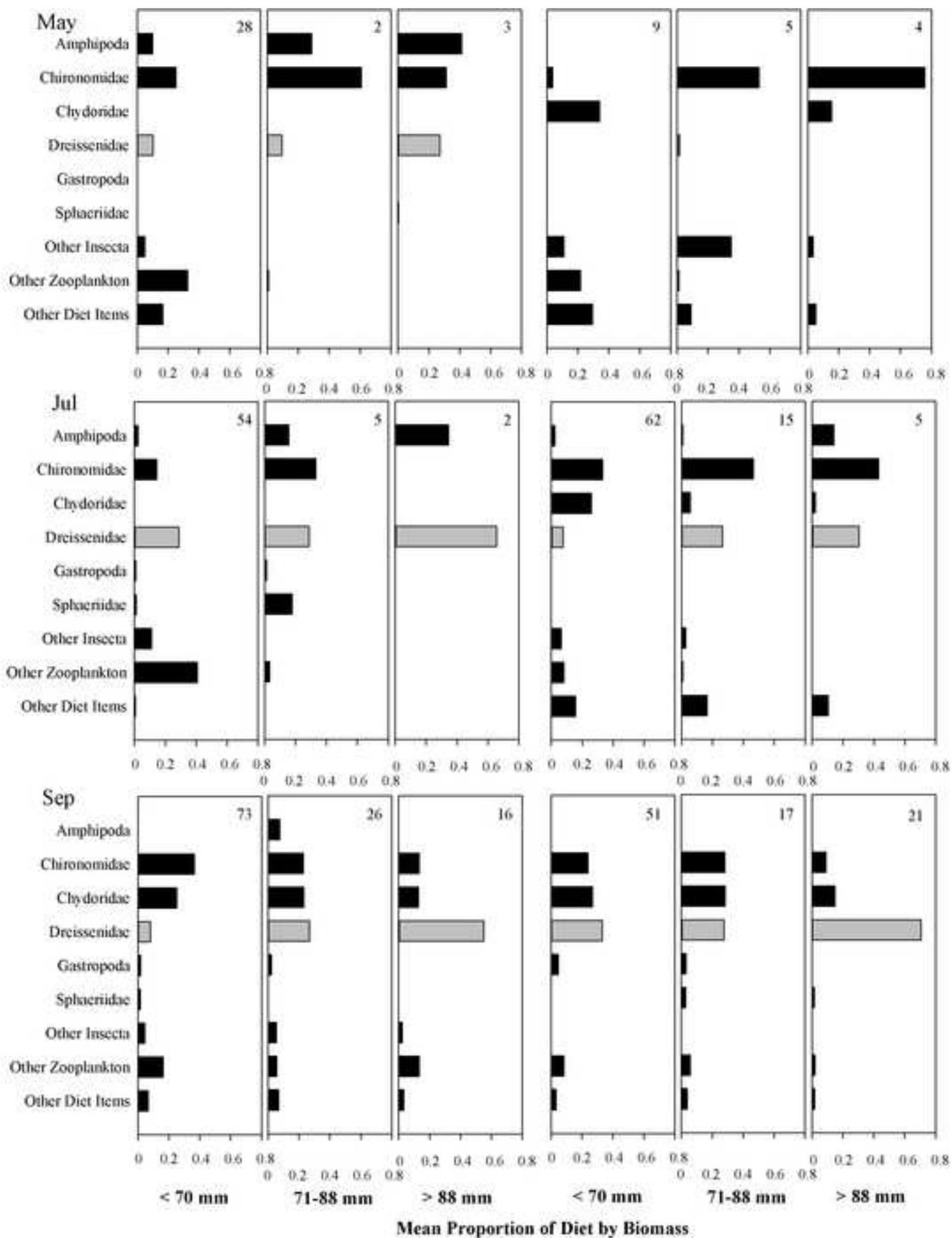


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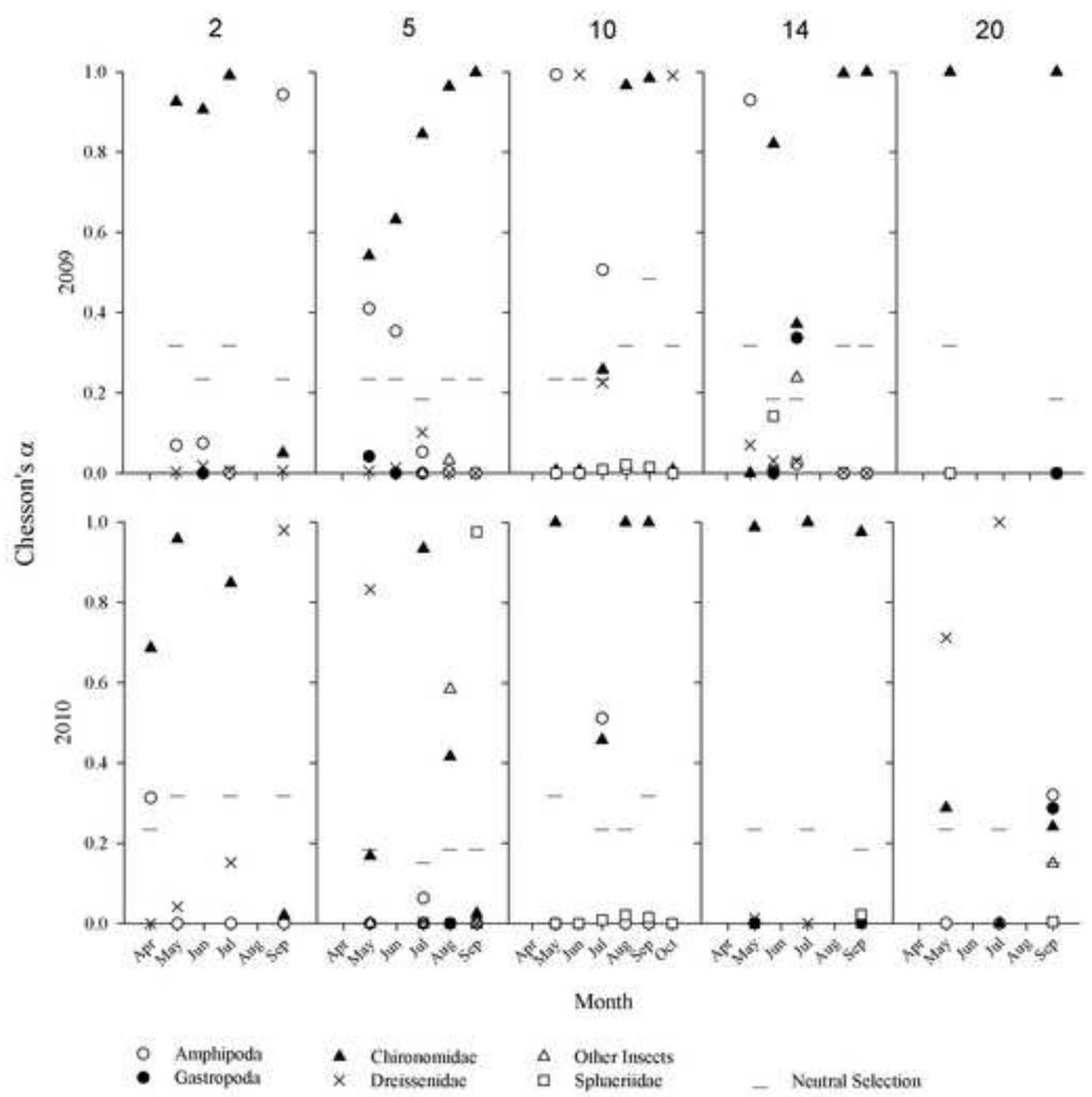


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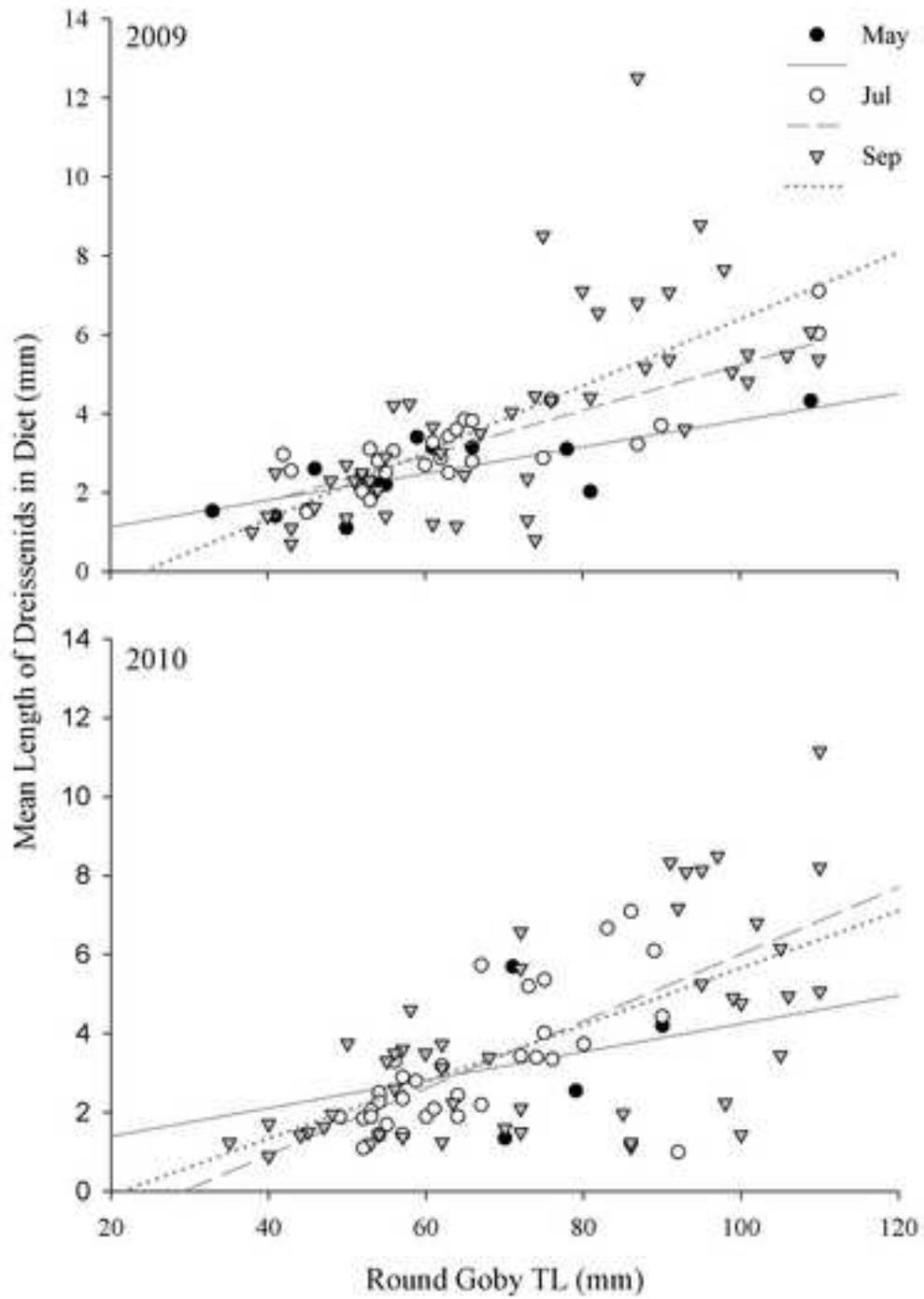
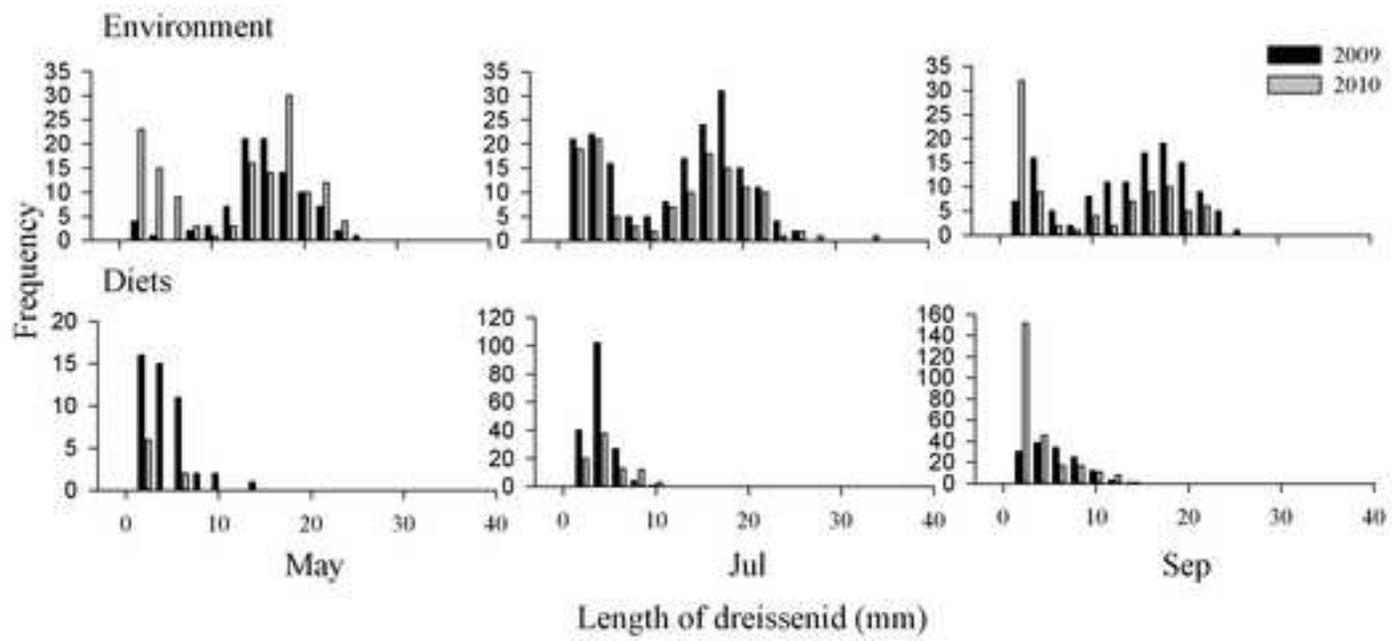


Figure 6
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